Figs and the Diversity of Tropical Rainforests

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Ficus *(Moraceae) is arguably one of the most important plant genera in lowland tropical rainforests. A brief review of tropical florulas also demonstrates that* Ficus *is the only ubiquitously diverse genus in lowland rainforests. Monoecious hemi-epiphytic figs, constituting independent radiations in each tropical biome, make up a significant proportion of species everywhere, but in Asia dioecious figs have diversified into a variety of niches, making the assemblages of this region especially speciose. Pioneer attributes have endowed figs with tremendous evolutionary flexibility, while long-range seed dispersal ensures that a high proportion of the regional species pool is represented in local assemblages. Large numbers of* Ficus *species are able to coexist because many are extremely rare as a result of limited recruitment opportunities, which limits competition. They are nevertheless able to breed at low densities because they possess an efficient, long-range pollination system. These factors are likely to be important in the diversity of other plant groups in the tropics.*

Keywords: biodiversity, Ficus, *rare niches, species coexistence, tropical rainforest*

Tropical rainforests are the richest terrestrial ecosystems on Earth, and explaining the coexistence of the diverse assemblages of species that inhabit them remains one of the fundamental challanges of tropical ecology. Recently, a great deal of theoretical attention has been focused on the problem, particularly following the publication of Hubbell's neutral theory (Hubbell 2001). An alternative approach, however, is to examine the biology of species that can be considered characteristic of tropical rainforests, and thereby derive an understanding of the traits that permit the evolution and coexistence of so many species. For example, trees of the family Dipterocarpaceae dominate the canopies of hyperdiverse rainforests in Southeast Asia, and thus a seminal review of their biology by Ashton (1988) revealed a great deal about how these forests support so many species. For this type of investigation, one might elect, as Ashton did, to study species that play a particularly important functional role in the tropical forest ecosystem. Alternatively, one might study those that belong to unusually large tropical genera; those that are typically rare, because rare species make up the bulk of the diversity in tropical forests; or perhaps those that possess peculiar habits more or less restricted to tropical forests. Figs (*Ficus,* Moraceae) would qualify on the basis of any of these criteria. As such, a discussion of their biology with respect to the diversity of species in tropical lowland rainforests is overdue.

Fig natural history

Globally, *Ficus* is a diverse genus (table 1), and figs are found in all lowland tropical rainforests (Berg 1989). In a global network of large-scale tree plots in the tropics, *Ficus* is the only genus recorded in every one of 18 plots in 14 countries (Losos and Leigh 2004). A number of researchers have commented on the extraordinarily low densities of many fig species (Todzia 1986, Michaloud and Michaloud 1987, Harrison et al. 2003); and figs possess diverse habits, many of which are characteristic of tropical rainforest plants such as hemi-epiphytes (a group that includes strangling figs and banyans), large woody climbers, and cauliflorous trees (inflorescences borne on the trunk; Harrison and Shanahan 2005). Globally, a staggering number of vertebrates—over 1200 species—feed on figs, and because at the population level figs fruit year-round, they may be critically important to wildlife when other fruits are not available (Shanahan et al. 2001). Many fig species are also pioneers and play a significant role in forest succession in the tropics (Corner 1967).

The genus *Ficus,* to which all figs belong, is defined by a unique pollination system (figure 1). Highly specific seed predator–pollinators, the fig wasps (Agaoninae, Agaonidae, Chalcidoidea), enter the urn-shaped inflorescence, where they pollinate and simultaneously lay eggs in some of the ovules. Approximately one month after the eggs are laid, the wasps' offspring emerge and, having mated, the female wasps disperse, carrying pollen from their natal fig. They must find a receptive inflorescence of the correct species of fig during

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Table 1. Global diversity of Ficus.

Region	Number of subgenera	Number of species
Indo-Pacific	6	> 500
Borneo	6	> 160
Papua New Guinea	6	> 150
Afrotropics	5	112
Neotropics	2	132
Global	7	> 800

Source: Updated from Berg (1989).

their short life spans (a few hours to 2 or 3 days in some species) to reproduce, and they thus fly large distances, farther than is known for any pollinator (> 10 kilometers [km]), using wind above the canopy (Nason et al. 1998, Harrison 2003).

Ficus is a monophyletic genus that originated approximately 80 million to 90 million years ago, although the main radiation of figs may not have occurred until later (Datwyler and Weiblen 2004). The sister lineage to the figs is the Castilleae tribe, with approximately 55 species (Datwyler and Weiblen 2004). Thus figs, with roughly 800 species (table 1), are substantially more diverse than their nearest relatives.

Large tropical plant genera

It is well known that some tropical plant genera contribute a disproportionate number of species to local plant assemblages. Such genera are pertinent to the question of how species coexist in tropical rainforests for a number of reasons. First, a few species-rich genera often make up a substantial part of the overall species richness in a tropical forest (Losos and Leigh 2004). Second, species within the same genus share a

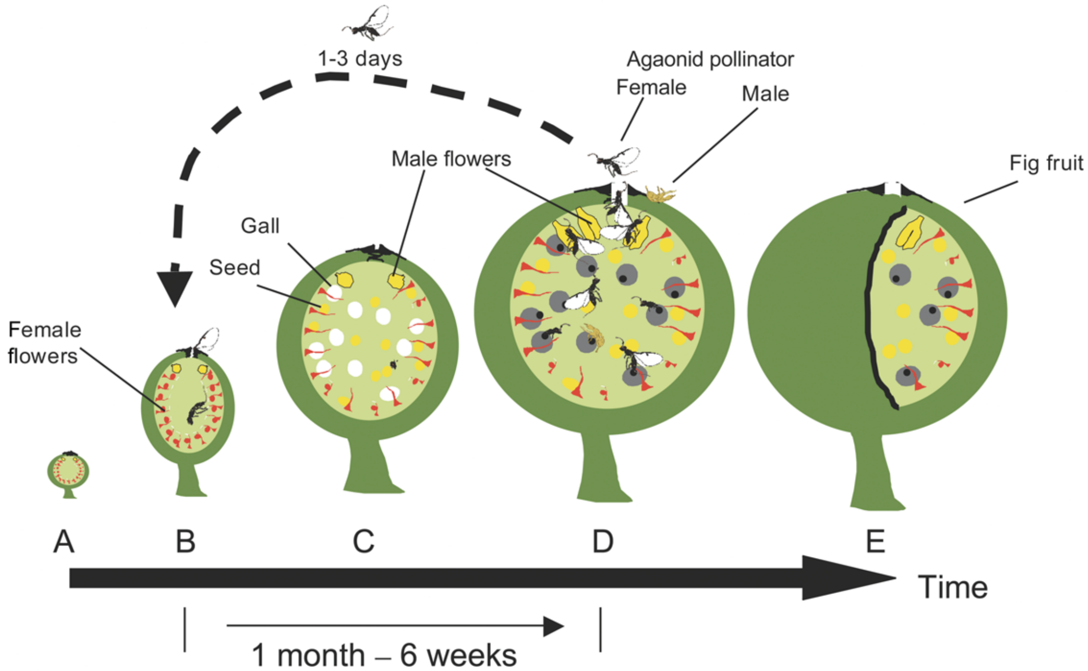

Figure 1. The development of a monoecious fig. The fig is a closed, urn-shaped inflorescence. Bracts that are tightly shut in the immature fig (stage A) loosen when it becomes receptive (stage B), allowing wasp pollinators to enter. Specificity is maintained in part by chemical cues and in part by the architecture of the bracts, which fit the wasp's head somewhat like a lock and key. Fig wasps possess several unique adaptations allowing them to enter the fig, including a series of ridges and teeth under the mandibles, and spikes on the third antennal segment and the fore and hind tibias, all of which act to prevent them slipping backward as they struggle through the bracts. Inside the fig, the wasps pollinate the uniovular female flowers and simultaneously lay their eggs on some ovules by inserting their ovipositors down the styles (stage B). Most wasps then die inside the fig. Ovules that receive an egg are induced to form a gall in which the wasp larva develops, while pollinated ovules missed by the wasp develop into seed normally (stage C). In dioecious figs (not illustrated), two types of inflorescence are borne on different plants. Female plants produce only seed, while male plants produce wasps and pollen. Approximately 4 to 6 weeks after the eggs are laid, the wasp offspring emerge from their galls (stage D). The wingless male wasps emerge first and mate with the gall-enclosed females. As the female wasps emerge, they collect pollen from male flowers which ripen at this time, and then disperse through a tunnel cut by the male wasps (stage D). The dispersing female wasps, which live from just a few hours to 2–3 days in some species, must find a receptive fig (stage B) of the correct species in order to reproduce. Following the emergence of the wasps, the wall of the fig softens, latex is withdrawn, and often other changes (e.g., in color and smell) follow, as the fig develops into a fruit structure (stage E). Globally, fig fruit are eaten by an extraordinarily diverse array of vertebrates (> 1200 species). Source: Shanahan and colleagues (2001).

Table 2. Lowland rainforest florulas used in this review.

Site	Latitude	Area (km^2)	Number of plant species	Source
Indo-Pacific				
Yakushima, Japan (extratropical)	30º N	500	383	Mitsuta and Nagamasu 1984
Hong Kong, China	22º N	1000	2145	Xing et al. 1999
Mount Kinabalu, Malaysia	6º N	700	4000	Beaman and Beaman 1990
Singapore Island, Singapore	1º N	48	2277	Turner et al. 1990
Krakatau, Indonesia (1951–1983)	6º S	33	455	Whittaker et al. 1989
Long Island, Papua New Guinea	5º S	330	305	Harrison et al. 2001
Crater Mountain, Papua New Guinea	7º S	2700	1200	Takeuchi 1999
Solomon Islands	10º S	27,600	4500	Whitmore 1966
Lamington, Australia (extratropical)	28º S	200	583	Queensland Government 1981
Afrotropics				
Forested area of Ghana	6º N	18,000	2120	Hall and Swaine 1981
Dzanga-Sangha, Central African Republic	3º N	4380	1100	Harris 2002
Kibale, Uganda	0º N	770	351	Lwanga 1996
Usambara Mountains, Tanzania	5º S	450	2973	Iversen 1991
Neotropics				
Santa Rosa, Costa Rica	11º N	372	603	Janzen and Liesner 1980
La Selva, Costa Rica	10º N	15	1668	Wilbur et al. 1994
Barro Colorado Island, Panama	9º N	15	1320	Croat 1978
Río Palenque, Ecuador	1º S	1	1200	Dodson and Gentry 1978
Ducke, Brazil	3º S	100	1200	Ribeiro et al. 1999
Cocha Cashu, Peru	12º S	10	1856[a]	Brako and Zarucchi 1993

a. Species total for lower Río Manu.

large number of traits, implying that they should have similar ecologies and thus exhibit a large degree of niche overlap. The coexistence of suites of such ecologically similar species is a special problem for the diversity of tropical rainforests, because standard niche theory predicts the competitive exclusion of species sharing similar niches. Third, some of the traits shared among species from diverse genera are presumably responsible for the evolution and maintenance of high species richness (Lovette et al. 2002). On the basis of plot data, genera such as *Psychotria* or *Piper* in the Neotropics (Fenner et al. 1997), *Drypetes* in Africa (Hall and Swaine 1981), and *Syzygium* in Asia (Turner et al. 1990) are commonly cited for their diverse local assemblages. However, scientists' knowledge of plant alpha-diversity in tropical rainforests is still patchy. Botanists are inclined to focus on particular taxa, while ecologists limit sampling to particular functional groups, such as trees. Moreover, regional or nationwide floral summaries are poor indicators of local species richness, because species vary widely in the extent of their ranges and in their degree of habitat specialization. Geographical variation also introduces an artifact into comparisons among genera, through differing traditions among taxonomists for lumping or splitting taxa. Nevertheless, over the past decade or so, a number of tropical rainforest florulas (floras of a particular site, such as a national park or research station) have been published. These lack the normal selective biases, as all taxa and life-forms are included, and the restricted geographical range substantially reduces taxonomic problems. A review of these florulas further underlines the importance of figs to tropical rainforests.

The florulas

I compiled florulas from 17 tropical lowland rainforest sites (Indo-Pacific [7], Afrotropics [4], Neotropics [6]; table 2). All available florulas that were substantially complete were included. Preliminary checklists were not considered, as these often contain the selective biases mentioned earlier. Three florulas (Usambara Mountains, Tanzania; Mount Kinabalu, Malaysia; and Crater Mountain, Papua New Guinea) incorporate large altitudinal gradients and may therefore over-represent genera with many montane species. Among the Indo-Pacific florulas, two are for island volcanoes and thus represent lowland rainforests in the process of reassembly. Krakatau, Indonesia, exploded in 1883, and Long Island, Papua New Guinea, erupted in approximately 1645; thus, these sites have had about 120 years and 360 years for biotic colonization, respectively. Also in the Indo-Pacific region, the environments of Singapore and Hong Kong have suffered very high levels of human disturbance from historical times until the present. The forest flora of Ghana (Hall and Swaine 1981) and the flora of the Solomon Islands (Whitmore 1966) were included for their completeness and importance to the botany of their respective regions, although the larger geographic areas covered slightly stretch the meaning of *florula*. Also, to investigate the latitudinal gradient in the Indo-Pacific region, I included florulas for two extratropical rainforests, Lamington National Park, Australia (28 degrees [°] south [S]), and Yakushima Island, Japan (30° north [N]). For the sake of comparability, I confine analyses to dicotyledonous genera. Some monocot genera are exceptionally diverse in tropical montane forests but exhibit much lower diversity in lowland forests, as these florulas and numerous studies of altitudinal gradients in species richness attest (Beaman and Beaman 1990).

A summary of the compilation, detailing the five richest genera at each site, is given in table 3. *Ficus* emerges as the only genus that is ubiquitously speciose in tropical lowland rainforests. In the Indo-Pacific region, *Ficus* was the most speciose genus at every tropical site, except in the strongly human-

Table 3. Comparison of plant species richness in the five largest dicot genera and the rank species richness for Ficus *at 19 lowland rainforest sites.*

	Five most speciose dicotyledonous plant genera (number of species), in rank order					
Site	**1**	**2**	**3**	**4**	**5**	***Ficus* rank**
Indo-Pacific						
Yakushima Island (extratropical)	*Polygonum* (15)	*Rubus* (11)	*Desmodium* (7)	*Euphorbia* (7)	*Ilex* (7)	7
Hong Kong	*Polygonum* (22)	*Ficus* (21)	*Lithocarpus* (18)	*Ilex* (16)	*Hedyotis* (15)	2
Mount Kinabalu	*Ficus* (82)	*Syzygium* (66)	*Litsea* (53)	*Elaeocarpus* (42)	*Elatosoma* (36)	1
Singapore	*Syzygium* (45)	*Ficus* (43)	*Memecylon* (22)	*Calophyllum* (18)	*Litsea* (18)	2
Krakatau	*Ficus* (22)	*Ipomoea* (5)	*Blumea* (4)	*Aeschynanthus* (3)	*Derris* (3)	1
Long Island	*Ficus* (31)	*Piper* (5)	*Dendrocnide* (4)	*Solanum* (4)	*Terminalia* (4)	1
Crater Mountain	*Ficus* (65)	*Cyrtandra* (24)	*Psychotria* (20)	*Syzygium* (20)	*Piper* (18)	1
Solomon Islands	*Ficus* (63)	*Syzygium* (37)	*Medillina* (19)	*Psychotria* (18)	*Piper* (15)	1
Lamington (extratropical)	*Parsonsia* (8)	*Solanum* (8)	*Ficus* (7)	*Acronychia* (6)	*Cinnamomum* (6)	3
Afrotropics						
Ghana	*Ficus* (32)	*Salacia* (24)	*Diospyros* (17)	*Drypetes* (13)	*Memecylon* (11)	1
Dzanga-Sangha	*Ficus* (21)	*Drypetes* (16)	*Clerodendrum* (12)	*Combretum* (12)	*Psychotria* (12)	1
Kibale	*Ficus* (17)	*Albizia* (7)	*Maytenus* (7)	*Rinorea* (5)	*Alchornea* (4)	1
Usambara Mountains	*Psychotria* (30)	*Ficus* (29)	*Vernonia* (26)	*Plectranthus* (27)	*Crotalaria* (24)	2
Neotropics						
Santa Rosa	*Cassia* (12)	*Mimosa* (10)	*Ipomoea* (8)	*Ficus* (7)	*Acacia* (6)	4
La Selva	*Piper* (41)	*Psychotria* (39)	*Miconia* (28)	*Inga* (20)	*Ficus* (16)	5
Barro Colorado Island	*Piper* (21)	*Psychotria* (20)	*Inga* (18)	*Ficus* (16)	*Miconia* (14)	4
Río Palenque	*Ficus* (25)	*Piper* (22)	*Solanum* (18)	*Peperomia* (15)	*Columnea* (9)	1
Ducke	*Pouteria* (41)	*Octea* (40)	*Licania* (30)	*Piper* (30)	*Protium* (29)	10
Cocha Cashu	*Ficus* (35)	*Inga* (26)	*Piper* (25)	*Pouteria* (21)	*Paullinia* (19)	1

altered environments (Hong Kong and Singapore), where it ranked second. In Africa, *Ficus* was the most diverse genus at three out of four sites and the second most diverse at the fourth, a site that has a substantial altitudinal gradient. *Ficus* rank varied more across the six Neotropical sites, but figs still appeared within the top 10 genera at all sites and usually within the top 5. Moreover, *Ficus* ranked number 1 at sites with the highest overall plant species richness.

Globally, no other genus compares to *Ficus.* Other diverse genera either have regionally restricted distributions or, as in the case of *Psychotria* or *Piper,* are especially diverse in only one region (table 3). Clearly there is something in the biology of *Ficus* that enables the repeated assembly of exceptionally diverse fig communities throughout the tropics.

Why has fig alpha-diversity been overlooked?

It is surprising that such high alpha-diversity of *Ficus* across the tropics should have passed unnoticed. However, the reasons for this oversight are apparent from the aforementioned biases in biologists' understanding of plant alpha-diversity in the tropics.

Sampling protocols are rarely broad enough to record all fig species at a site, because of the variety of plant habits evidenced by the genus (Harrison and Shanahan 2005). Most information about tropical plant diversity comes from tree plots, and in all tropical lowland rainforests a minority of fig species are trees.

The very low densities of many fig species (table 4) mean that extensive collecting efforts are required to record a reasonable proportion of species. Even more complete florulas often poorly estimate fig diversity. For example, in the Usambara Mountains, Iversen (1991) collated records for 2973 plant species, an extraordinarily long list for the Afrotropics, but recorded only 20 fig species. Later collecting that specifically targeted figs found a further 9 species (Jean-Yves Rasplus, INRA, Montpellier, France, personal communication, 2005). In the forest flora of Ghana, only two figs were classified as common species (meaning that they were recorded in at least 4 out of the total of 168 plots), although *Ficus* was substantially the most diverse genus (Hall and Swaine 1981). The rarity of many figs also means that small areas do not harbor a full complement of species. For example, Barro Colorado Island (15 km^2) has 16 fig species (Croat 1978), but when similar habitat in the surrounding Lake Gatun area is included, at least two more species are added. Given that several of the Neotropical florulas are for very small areas, it is possible the diversity of *Ficus* has been underrepresented at these sites (tables 2, 3; Janzen and Liesner 1980).

Finally, fig species often have very large ranges and the turnover of species with distance is therefore low. Floras for larger geographic areas thus underestimate fig alpha-diversity. For example, in Singapore, *Syzygium* and *Ficus* have roughly equal species totals (table 3), but when the flora is expanded to include the rest of Peninsula Malaysia, *Syzygium* (195 spp.) has almost double the number of species as *Ficus* (102 spp.; Turner et al. 1990). Similarly, *Ficus* is the most diverse genus at Cocha Cashu, Peru, but does not rank within the top five genera in the national flora (Fenner et al. 1997). In contrast, *Piper,* which ranked third at Cocha Cashu, ranks number 1 in the national flora, with three times as many species in Peru (429 spp.) as there are fig species in the Neotropics (Berg 1989, Fenner et al. 1997).

Of course, the alpha-diversity of other genera with multiple life-forms or rare, widespread species must also have been previously underestimated. However, figs are exceptional in the degree to which these traits are exhibited.

Evolutionary and biogeographic patterns of *Ficus* alpha-diversity

Fig alpha-diversity varies geographically reflecting the divergence of major clades within the genus and concurrent evolution of diverse life-histories (figures 2, 3). In the Neotropics and Afrotropics, *Ficus* alpha-diversity is comparable, while similar sites in the tropical Indo-Pacific region have more than twice as many species (table 3). In the Neotropics and Africa, monoecious hemi-epiphytes (sections *Americana* and *Galoglychia,* respectively; figure 1) constitute 75% or more of the fig species in any particular assemblage, with monoecious mid- to late-succession pioneer trees making up the remainder of species in the Neotropics (section *Pharmacosycea*) and most of the remainder in Africa (section *Sycomorus;* figure 2, table 5). However, in the Indo-Pacific region, in addition to the monoecious hemi-epiphytes, there have been several other significant radiations, most notably of dioecious figs that are absent from the Neotropics and poorly represented in Africa (figure 2). These dioecious figs have diverged ecologically into a broad spectrum of niches (figure 2, table 5; Harrison and Shanahan 2005). Farther east, in the Solomon Islands and New Caledonia, there has been an extraordinary radiation of the monoecious *Oreosycea* figs to occupy niches from early-successional pioneers to canopy trees (table 5; Corner 1967). Elsewhere, *Oreosycea* figs are emergent trees and often extremely rare.

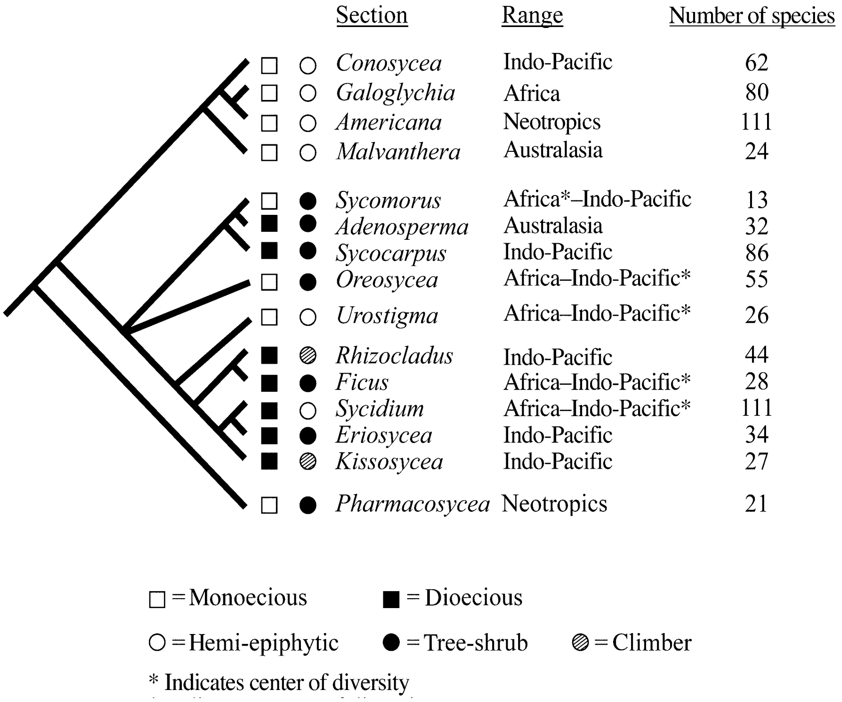

Figure 2. Phylogeny of genus Ficus*, showing the distribution of breeding systems, life-forms, taxonomic sections, geographic range, and species richness. The genus is monophyletic and approximately 80 million to 90 million years old (Datwyler and Weiblen 2004).* Pharmacosycea *is the outgroup to all other figs and is strictly Neotropical. Below this are two major clades: (1) a clade of monoecious hemi-epiphytic figs, with a single independent lineage in each region plus* Malvanthera *in Australasia, and (2) a more complicated Paleotropical clade with both monoecious and dioecious lineages. In this latter group,* Sycomorus *is essentially African, with 12 species in Africa (of which 7 are endemic to Madagascar or Indian Ocean islands) and only 1 species in the Indo-Pacific region; all the other lineages are primarily Indo-Pacific, although* Ficus *(1 sp.),* Sycidium *(8 spp., of which 5 are endemic to Madagascar or Indian Ocean islands),* Oreosycea *(4 spp., of which 2 are endemic to Madagascar), and* Urostigma *(7 spp., of which 5 are endemic to Madagascar or Indian Ocean islands) have African members. In the genus* Ficus*, monoecy is ancestral. Dioecy appears to have evolved twice and been lost three times—once leading to the* Sycomorus *figs, and twice in two isolated species in section* Sycocarpus*.* Ficus *evidences greater diversity of growth habits than any other genus (figure 3). Hemi-epiphytes have most likely evolved four times within the genus (once in an isolated* Pharmacosycea *fig), while climbing figs have probably evolved twice. However, these basic categories do not adequately represent this aspect of* Ficus *diversity (Harrison and Shanahan 2005). Redrawn from Jousselin and colleagues (2003).*

Superimposed on this basic phylogenetic map, several other biogeographic patterns are evident. First, there is a strong latitudinal gradient in the relative diversity of *Ficus.* At Lamington (28° S) and Yakushima (30° N), *Ficus* ranked just third and seventh, respectively (table 3). The restriction of most fig species to tropical climates is most likely a result of their unique pollination system. Because pollinators depend on receptive fig inflorescences for reproduction, year-round availability of fig inflorescences is a necessary condition for the mutualism to persist. The few fig species in strongly seasonal areas that preclude year-round plant growth and reproduction have highly derived phenological patterns.

Second, in the forests of tropical volcanic islands that are recovering from life-annihilating eruptions, figs are especially speciose relative to other genera. On Krakatau, *Ficus* has over four times as many species as the next genus, while on Long Island the difference is even greater (table 3; Whittaker et al. 1989, Harrison et al. 2001). Indeed, it has been suggested that the establishment of figs is a critical phase in the reassembly of forests on such islands, with plant colonization accelerating after the first figs begin to fruit and thereby to attract seed dispersers carrying the seeds of other species in their guts (Thornton et al. 2001). Both Krakatau and Long Island lie more than 50 km from the coasts of their respective source communities. Thus, their successful colonization by *Ficus* indicates that the genus has exceptional long-distance seed dispersal, despite its dependence on animal vectors.

Table 4. Densities of hemi-epiphytic figs in different rainforests (individuals with roots connected to the ground).

Country	*Ficus* section	Number of species	Density (individuals per hectare) Minimum	Maximum	Mean	Source
Indo-Pacific						
Thailand	*Conosycea*	15	–	–	0.27	Data available from author
Borneo	*Conosycea*	25	0.02	0.46	0.12	Harrison et al. 2003
Afrotropics						
Ivory Coast	*Galoglychia*	19	0.05	0.91	0.25	Michaloud and Michaloud 1987
Ghana	*Galoglychia*	27	0.01	0.79	0.14	Hall and Swaine 1981
Neotropics						
Panama	*Americana*	9	0.05	0.80	0.33	Todzia 1986
Ecuador[a]	*Americana*	10	0.02	0.12	0.06	Data available from author

a. Only free-standing individuals.

Moreover, the successful fruiting of figs on the islands indicates that their fig wasp pollinators have also colonized: strong evidence that fig dispersal is not limited by the plants' highly specific pollination system. Given that we know fig wasps are capable of routine long-distance dispersal, this is not surprising, but the possession of highly specific mutualistic interactions has often been suggested as a factor limiting species distributions. Obviously, a capacity for long-distance seed dispersal explains, at least in part, why so many fig species have large ranges. It also means that dispersal limitation will be a much less significant factor in determining the composition of local assemblages than is the case for most other plant genera. This is evident from the high proportion of figs from regional species pools in each of the florulas (tables 1, 3): 27% of Neotropical fig species occur at Cocha Cashu; 34% of continental African species occur in the Usambara Mountains; and 53% of Borneo's fig species are found on Mount Kinabalu.

Third, the diversity of fig species relative to other plant genera is lower in highly human-altered environments than it is elsewhere (table 3). Hong Kong has only 21 fig species (Xing et al. 1999), but in undisturbed forests at Xishuangbanna, on the Chinese mainland, there are over 60 species. Similarly, Singapore has just 43 fig species, whereas one would expect to find 60 to 70 species coexisting in forests on the Malay Peninsula (Turner et al. 1990). Figs must have suffered a higher rate of extirpations than other diverse plant genera in Hong Kong and Singapore.

At first this appears to conflict with the observation above that figs are a critical component of regenerating tropical forests. However, the figs that have colonized Krakatau and Long Island are mostly common species with broad ecological tolerances (Thornton et al. 2001). Indeed, the islands have seven species in common (37% of Krakatau's fig flora), despite being separated by more than 1000 km and by a major biogeographic boundary (Wallace's line). Conversely, the species that are missing from Hong Kong and Singapore are rare ecological specialists, such as hemi-epiphytic figs that colonize emergent trees and depend on large vertebrates, especially hornbills, to disperse their seeds (Harrison et al. 2003, Harrison and Shanahan 2005). Hong Kong and Singapore have few areas with large trees and most of the large frugivores have been extirpated.

Finally, in the Neotropics the relative species richness of *Ficus* compared with other genera varied more among sites than it did in the African and Indo-Pacific regions. Nevertheless, at Cocha Cashu and Río Palenque, *Ficus* was still the most speciose genus (table 3). Both sites have extremely high overall plant diversity, which probably results from the unusually high fertility of the soils. In contrast, the central-Amazonian soils at Ducke, where *Ficus* ranked only 10th, are extraordinarily infertile (Ribeiro et al. 1999). Commenting on local distributions elsewhere, some authors have noted a paucity of figs on less fertile soils (Corner 1967, Harrison and Shanahan 2005). High nutrient and water availability may be necessary to support typically high assimilation rates (Zotz et al. 1995) and hence may restrict many fig species to more fertile sites.

In summary, a phylogenetic and biogeographic perspective considerably refines our understanding of *Ficus* alpha-diversity. Monoecious hemi-epiphytic figs, constituting independent radiations in each region (figure 2), contribute substantially to *Ficus* alpha-diversity everywhere. However, in the Indo-Pacific, several dioecious lineages have radiated and diversified ecologically, resulting in exceptionally rich fig assemblages in this region. Fig diversity exhibits a pronounced latitudinal gradient and the genus is more or less restricted to tropical and subtropical zones. Figs are exceptional long-distance colonizers and as a result are a significant component of plant communities on volcanic islands. However, the rarity of many species makes them prone to disturbance. Fig alpha-diversity may also be linked to soil fertility, with fewer species apparently able to colonize impoverished soils, possibly because of typically high assimilation rates.

Why are figs ubiquitously speciose in tropical lowland rainforests?

High alpha-diversity in any genus has both a historical and an ecological context. What factors fostered the evolutionary radiation of species within the genus, and what factors permit the assembly and coexistence of multiple species? However, before proceeding further, the issue of whether or not high alpha-diversity in *Ficus* is merely an artifact of taxonomy needs to be addressed.

Table 5. Phylogenetic distribution of Ficus *alpha-diversity at 19 rainforest sites.*

Site	Pharmacosycea	Conosycea	Galoglychia	Americana	Malvanthera	Sycomorus	Adenosperma	Sycocarpus	Oreosycea	Urostigma	Rhizocladus	Ficus	Sycidium	Eriosycea	Kissosycea	Number of *Ficus* sections
Indo-Pacific																
Yakushima	–	1	–	–	–	–	–	–	–	1	2	1	–	–	–	5
Hong Kong	–	1	–	–	–	–	–	3	2	2	4	4	2	3	–	21
Mount Kinabalu	–	17	–	–	–	1	–	16	2	–	11	2	18	9	6	82
Singapore	–	12	–	–	–	1	–	6	1	2	5	1	8	4	3	43
Krakatau	–	4	–	–	–	1	–	6	2	–	–	1	6	2	–	22
Long Island	–	2	–	–	4	–	2	9	2	3	–	–	9	–	–	31
Crater Mountain	–	4	–	–	5	–	13	15	5	–	8	–	12	–	3	65
Solomon Islands	–	5	–	–	3	–	5	18	8	3	5	–	16	–	–	63
Lamington	–	–	–	–	4	–	–	–	–	1	–	–	2	–	–	7
Afrotropics																
Ghana	–	–	27	–	–	3	–	–	1	–	–	–	1	–	–	32
Dzanga-Sangha	–	–	18	–	–	2	–	–	–	–	–	–	1	–	–	21
Kibale	–	–	11	–	–	3	–	–	1	–	–	–	2	–	–	17
Usambara Mountains	–	–	21	–	–	4	–	–	–	2	–	–	2	–	–	29
Neotropics																
Santa Rosa	1	–	–	6	–	–	–	–	–	–	–	–	–	–	–	7
La Selva	3	–	–	13	–	–	–	–	–	–	–	–	–	–	–	16
Barro Colorado Island	4	–	–	12	–	–	–	–	–	–	–	–	–	–	–	16
Río Palanque	3	–	–	22	–	–	–	–	–	–	–	–	–	–	–	25
Ducke	2	–	–	17	–	–	–	–	–	–	–	–	–	–	–	19
Cocha Cashu	6	–	–	29	–	–	–	–	–	–	–	–	–	–	–	35

Note: The taxonomic arrangement of sections follows figure 2.

Taxonomy. It is possible that exceptionally high diversity in a genus merely results from a genus concept that is too broad, lumping several disparate lineages under a single name. For example, globally, *Piper* comprises several divergent clades that could be treated as separate genera (Jaramillo and Manos 2001). However, molecular phylogenies both support maintaining *Ficus* as a single entity and, moreover, suggest the genus may have radiated quite recently (Datwyler and Weiblen 2004). Furthermore, high alpha-diversity in figs results largely from the coexistence of closely related species in one or just a few clades (table 5).

Evolutionary diversification in *Ficus*. Figs have evolved to encompass an extraordinary breadth of plant life histories (figure 3). Plant habits range from shrubby pioneers 1 to 2 meters (m) high, through small to emergent trees, climbers, epiphytes, and hemi-epiphytes, to banyans with canopies greater than 150 m in diameter (Harrison and Shanahan 2005). Life spans similarly vary from a few years in pioneer shrubs to over 1000 in the biggest banyans (the oldest tree of known planting date is a fig, *Ficus religiosa,* planted at Anuradhapura, Sri Lanka, by King Tissa in 288 BC; Lewington and Parker 1999). Seed dispersal syndromes and correlated traits such as fruit placement and flowering phenology also vary substantially (Shanahan et al. 2001, Harrison and Shanahan 2005). There are two breeding systems (monoecy and dioecy), and coevolution with highly specific pollinators has led to considerable variation in floral traits (Herre 1989, Kjellberg et al. 2001). Thus, species across the genus as a whole occupy an extremely broad spectrum of niches.

Figs possess many traits typical of pioneer plants—small seeds, high assimilation and growth rates, high fecundity, and flexible rooting habits—that have clearly been fundamental in promoting their evolutionary diversification. For example, many species, in particular the hemi-epiphytic figs, have stringent microsite requirements. Small seeds and high fecundity are essential to cover such infrequent and widely dispersed recruitment opportunities. Even with their huge crops of fruit, and with each fruit containing tens to hundreds of seeds, hemi-epiphytic figs appear to have enormous obstacles to recruitment, and potential microsites for colonization in the canopy are strongly undersaturated (Laman 1996).

Small seeds have also endowed figs with tremendous evolutionary flexibility with respect to seed dispersal syndromes (Shanahan et al. 2001). A fruit cannot be smaller than the seed it contains, and larger seeds require better protection against seed predators. Therefore, increasing seed size restricts fruit design. In fact, the initial evolution of smaller seeds was probably a critical step in the history of *Ficus.* Fig wasps are seed predator–pollinators. To benefit the fig, there must be a profitable exchange between pollination services rendered, through delivery of pollen by dispersing female fig wasps, and seeds destroyed. Small seeds limit the cost inflicted, as each pollinator larva only destroys one seed, and large numbers of seeds per inflorescence ensure that a certain proportion escape predation. It is interesting to note that members of the Castillae tribe, which have involucrate, incipient fig inflorescences but have never evolved a similar seed predator–pollinator mutualism, all have much larger seeds (Datwyler and Weiblen 2004).

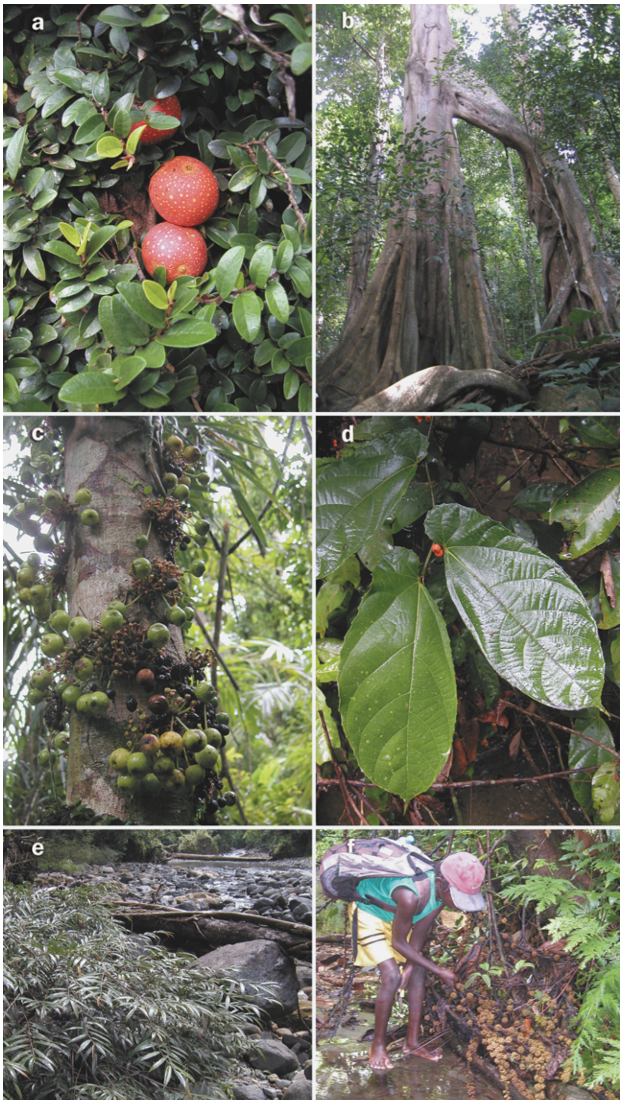

Figure 3. Some growth habits of Ficus. *(a)* **Ficus aurantiacea** *Griff. (section* Kissosycea*), a bole climber. (b)* **Ficus kerkhovenii** *Valeton (section* Conosycea*), a free-standing strangler. (c)* **Ficus fistulosa** *Reinw. ex Bl. (section* Sycocarpus*), a cauliflorous pioneer. (d)* **Ficus fiskei** *Elmer (section* Sycidium*), an understory hemi-epiphyte. (e)* **Ficus rivularis** *Merrill (section* Sycocarpus*), a rheophytic shrub. (f)* **Ficus minahassae** *Miq. (section* Sycocarpus*), a geocarpic pioneer. Photographs: Rhett D. Harrison.*

The ability of figs to develop aerial roots, presumably an adaptation to colonize rocky habitats, has also been important in the evolution of *Ficus.* Indeed, the divergence of several major lineages within the genus is associated with a change in growth habit (figure 2). Hemi-epiphytes, for example, have probably evolved four times and are among the most speciose lineages.

Finally, like all Moraceae, figs are protected by latex, a costly but efficient defense against herbivores. Plant families that produce latex for defense are more speciose than those that do not (Farrell et al. 1991), and figs may be better able to afford the expense of latex production, in terms of carbon allocation, because of their very high assimilation rates (Zotz et al. 1995). Herbivory is especially prevalent in gaps (Coley and Barone 1996), and defense by latex may be particularly important for fig inflorescences, relatively few of which are lost to herbivores (Bronstein 1988).

One might ask why, if these pioneer traits have been so important in the evolutionary diversification of *Ficus,* are other pioneer genera not as diverse? First, some tropical pioneer genera, such as *Cecropia* (approximately 75 spp.) in the Neotropics or *Macaranga* (approximately 300 spp.) in Africa and Asia, are quite diverse. Second, figs combine basic pioneer traits with other less common ones, such as flexible rooting habits and latex production, which has enabled them to evolve far beyond a normal pioneer niche. Indeed, over half of all fig species are hemi-epiphytes (figure 2).

Species coexistence. As mentioned earlier, in the Indo-Pacific region, fig assemblages are composed of several diverse lineages (figure 2), and thus fig species within the same assemblage may have quite divergent ecologies (table 6; Harrison and Shanahan 2005). This explains the exceptionally high diversity of fig assemblages in this region, as compared with the Neotropics or Africa. Nevertheless, even in the Indo-Pacific region, most of the diversity results from just a few speciose lineages, and in the Neotropics and Africa, only the monoecious hemi-epiphytes contribute significantly to high alpha-diversity.

Species within a lineage tend to share broadly similar ecologies (table 6), probably determined largely by their growth habits (Jousselin et al. 2003). However, wherever ecological studies have been conducted, closely related species in the same assemblage have been found to segregate along simple niche axes. For example, in Borneo, hemi-epiphytic figs colonize hosts from a particular canopy stratum. Thus, different species were found on understory, subcanopy, canopy, and emergent hosts (Harrison et al. 2003). Among early-succession pioneer figs (section *Sycocarpus*) from the same forests, maximum stem diameter, a good indicator of life-history strategy in trees, varies continuously and by almost an order of magnitude across all seven species (1.9 to 10.1 centimeters [cm]; Harrison and Shanahan 2005). Species may also differ in reproductive biology. For example, in a community of 12 monoecious hemi-epiphytic figs in Panama, species vary more or less continuously in female flower number, male flower number, seed and pollinator size, and average number of pollinators entering a fig (Herre 1989). Similarly, there are often substantial differences in fruit size among fig species with the same general seed dispersal syndrome (Kalko et al. 1996, Shanahan et al. 2001).

Thus, it is tempting to explain the coexistence of closely related fig species in terms of basic niche theory. However, many fig species are so rare (table 4) that competition is unlikely to be an important process. For example, in Borneo, only 1.77% of trees bigger than 30 cm in diameter were colonized by a hemi-epiphytic fig (Harrison et al. 2003). Even allowing

Table 6. *Comparison of ecological traits among figs of different sections at Lambir Hills in Borneo.*

Section	Breeding system	Growth form	Density (per hectare)	Phenology: Percentage of plants fruiting	Phenology: Fruiting frequency (crops per year)	Crop size	Fig placement	Principal seed disperser (number of species per crop)
Conosycea	Monoecious	Hemi-epiphyte	0.02–0.46	73	0.75	$10^{3–5}$	Among foliage	Canopy birds and mammals, bats (10–32)
Sycocarpus	Dioecious	Small tree	0.02–15.00	100	4.06[a]	$10^{0–2}$	Cauliflorous/ geocarpic	Terrestrial mammals, bats (1–3)
Oreosycea	Monoecious	Large tree	0.25	–	–	–	Among foliage	Bats (?)
Urostigma	Monoecious	Hemi-epiphyte	0.06	–	–	$10^{3–6}$	Among foliage	Canopy birds and mammals, bats (?)
Rhizocladus	Dioecious	Climber	0.04–0.10	81	1.13	$10^{3–4}$	Cauliflorous	Understory birds (4)
Ficus	Dioecious	Shrub/epiphyte	0.04–5.38	–	–	$10^{0–2}$	Among foliage	Understory birds (?)
Sycidium	Dioecious	Hemi-epiphyte	0.02–0.25	100	2.80	$10^{2–3}$	Among foliage/ cauliflorous	Understory birds (6–10)
Eriosycea	Dioecious	Small tree	–	98	3.51	$10^{1–3}$	Among foliage	Understory birds (8–18)
Kissosycea	Dioecious	Climber	0.04–0.29	83	2.55	$10^{1–2}$	Cauliflorous	Arboreal mammals, bats (2–4)

Note: The taxonomic arrangement follows figure 2. Figures for density and crop size indicate the range across species. Figures for percentage of plants fruiting and fruiting frequency indicate the mean across species.

a. Several species are completely asynchronous.

Source: Harrison and Shanahan 2005.

for higher densities of seedlings, competition is unlikely to be of much consequence. Only among the early-succession pioneers (sections *Ficus* and *Sycocarpus*), where densities are higher and several species may be found in close proximity (Harrison and Shanahan 2005), is it reasonable to postulate that competition is a significant ecological process. Among figs that are typically rare, such as the monoecious hemi-epiphytes, specialization probably reflects a process of ecological filtering, in which trade-offs in allocation or ecophysiological traits force species to adopt narrow niches (Wright 2002, Harrison et al. 2003). However, the colonization of niches with low levels of competition can itself explain species coexistence. High alpha-diversity in several other plant groups has been similarly allied to niches with little competition. For example, among monocots, epiphytic orchids can form phenomenally speciose assemblages (Beaman and Beaman 1990), and the high alpha-diversity of understory shrubs (e.g., *Psychotria*) has also been attributed to a scattered, low-density and therefore low-competition niche (Wright 2002).

In summary, although there is good evidence for fine niche differentiation among closely related fig species, competition is likely to be a significant ecological process in only a few lineages. Many figs, typified by the monoecious hemi-epiphytes, are simply too rare. Coexistence is therefore most likely explained by the fact that they occupy niches with low levels of competition.

Fig pollination. Figs have a highly specific, supremely efficient long-range pollination system. Despite the distances that often exist between individuals of the same species, a very high proportion of inflorescences are pollinated in most species. Moreover, synchronous development of inflorescences within a crown, combined with asynchrony of flowering between individuals, ensures outcrossing and thus maintains high levels of heterozygosity (Nason et al. 1998). Only in a few species or in marginal environments are fig trees pollen limited (Bronstein 1988, Harrison 2000). By comparison, pollination of most other rainforest plants is notoriously inefficient, and a large proportion of ovules, lacking outcrossed pollen, are aborted (Roubik 1993).

Fig pollinators can travel long distances using wind above the canopy (Harrison 2003) and then home in on receptive trees using volatile cues. Wind pollination is rare in tropical forests, because as the distance between conspecific plants increases, the efficiency of randomly wafting pollen across the canopy decreases exponentially. Wind-pollinated plants in tropical forests, such as *Casuarina* in Asia, which forms dense stands along beaches, or *Cecropia* in the Neotropics, which occurs in clumps in forest gaps, are exceptions that prove the rule. Biotic pollination, however, is expensive, as plants pay for the service in the form of floral rewards. Social bees, for example, which pollinate about 20% to 30% of plants in tropical forests, assess the richness of the reward against the energy expended in foraging. Thus, as plant species become increasingly rare they must either invest more in floral rewards or endure lower rates of outcrossing (Roubik 1993).

In figs, wind provides the energy for long-distance pollen transport, but the inefficiencies of wind pollination are circumvented by usurping the reproductive interests of fig pollinators to seek out receptive inflorescences. The efficiency of this system has enabled figs to occupy very rare niches and thus is an important factor to consider in understanding the high alpha-diversity of fig assemblages. An ability to outcross at very low population densities may also have lowered extinction rates over evolutionary time scales and so have contributed to the diversity of regional species pools in *Ficus.*

The high specificity of the fig pollination system also enables species in diverse assemblages to avoid problems of cross-pollination. However, fig pollination is not as absolutely species specific as it was once thought to be. Wherever the matter has been investigated in sufficient detail, a proportion of fig species (20%–30%) have been found to host multiple pollinator species. Most cases are allopatric, but an increasing number of examples have been found of multiple pollinator species living in sympatry. These cases involve two to four pollinator species sharing a single host. Thus, pollination is still species specific. However, a number of cases of pollinators utilizing two hosts have also been recorded, and Machado and colleagues (2005) recently reported on the discovery in Panama of three fig species sharing the same pollinator, along with evidence of historical introgression among figs. Indeed, these authors go on to suggest that introgression may be an important engine for generating genetic diversity in figs, ultimately contributing to high species richness in the genus. At the very least, the fact that the occurrence of multiple pollinator species on the same host fig is not uncommon provides a ready mechanism for speciation, as shifts in specificity among pollinator species could quickly create gene-flow barriers between incipient species.

Figs as a model for the diversity of tropical forests

To what extent does what we have learned about the diversity of figs confer with our understanding of species diversity in other tropical plants? Families or genera that demonstrate evolutionary flexibility tend to be more diverse (Ricklefs and Renner 1994, Fenner et al. 1997, Lovette et al. 2002). Moreover, *Piper,* which is globally a very large genus, is often a pioneer plant and, like *Ficus,* has diverse rooting habits (Jaramillo and Manos 2001). As mentioned above, plants that occupy niches with low levels of competition, such as the epiphytic orchids or understory *Psychotria,* also often form speciose local assemblages (Wright 2002). And, obviously, increased long-distance seed dispersal (reduced dispersal limitation) will result in a greater proportion of regional species in local assemblages (Hubbell 2001). What we learn from figs, therefore, reinforces these earlier ideas about tropical diversity. However, outside of the small group of people who study pollination in tropical rainforests (Roubik 1993), few appear to consider it a very significant aspect of tropical plant diversity. Most theoretical approaches, for example, simply ignore pollination (Hubbell 2001). But given the importance of outcrossing in tropical rainforests, plants can only be as rare as their pollinators allow them to be, and hence pollination is potentially a major factor limiting plant species richness. The pollination system in figs permits species to exist at extremely low densities, presumably levels untenable for most other plants, and is thus central to figs' ability to form speciose assemblages.

Figs also call into question other ideas about tropical diversity. For example, it has been argued that high species richness in tropical rainforests is promoted by benign conditions that permit escalating "arms races" between plants and their natural enemies, forcing plants to escape through rarity. However, in hemi-epiphytic figs, which are among the rarest plants in tropical forests, low densities are the result of specialized microsite requirements. Many other plants in tropical rainforests may also be rare as a result of limited recruitment opportunities. For example, shade-tolerant canopy tree seedlings can persist for years, barely growing, while they wait for the right conditions to begin their ascent toward the canopy (Delissio et al. 2002). In studies of species coexistence, fine niche differentiation among closely related species is often taken to imply character displacement through competitive interactions. However, as was found among hemi-epiphytic figs in Borneo, trade-offs in allometry or ecophysiology across an abiotic gradient can also force species to specialize. Thus, although the segregation of species across abiotic gradients may contribute to the overall diversity of species in the landscape, one cannot assume that niche differentiation through competition is the mechanism behind species coexistence.

Ficus illustrates several attributes that contribute to the assembly of diverse plant communities in the tropics. Evolutionary flexibility, derived from a pioneer habit, has generated diverse regional species pools, and exceptionally long-range seed dispersal enhances the diversity of local assemblages. Occupancy of niches with low levels of competition enables multiple species to coexist, and an efficient long-distance pollination system permits rare species to breed. These attributes are likely to be important in the diversity of many other plant groups in tropical rainforests.

Future research directions in *Ficus*

There has been an exponential growth in the number of papers appearing on *Ficus* in the past three decades or so. Figs are an ideal model for comparative study, with numerous co-occurring species; diverse ecologies; a variety of symbionts, including highly specific pollinating and nonpollinating wasps, bacteria (*Wolbachia*), nematodes, ants, and vertebrate seed dispersers; easily counted units (flowers, seeds, and wasps) for assessing reproductive investment; and a highly conserved pollination system. Thus, establishing detailed molecular phylogenies for figs and their wasp associates has been and will continue to be a major focus of research.

So far researchers understand very little about the evolutionary patterns of colonization and radiation for the vast majority of nonpollinating wasp genera, and their community ecology remains largely unstudied (we still do not have a single quantified food web). The discovery of increasing numbers of cases of figs with multiple pollinator species has also opened the door to numerous new possibilities for studies on the balance of the fig–fig pollinator interaction. Tropical biologists, especially those working on figs, are generally well aware of these possibilities.

The findings of this study demonstrate that *Ficus* is also a fascinating genus for the study of plant ecology. Coexistence in speciose assemblages, evolutionary divergence into diverse ecologies, and the existence of unusual growth forms all lend interest to this field. Our understanding of the evolutionary biology of figs is also currently hampered by a poor knowledge of their ecology. Thus far, evolutionary studies have been confined to a paltry set of traits, namely breeding system, growth form, and pollination mode (active or passive); divorced from its ecological context, the interpretation of trait changes has been of limited value. How and to what extent the broader ecology of a species constrains, for example, the fig–fig pollinator interaction, the community structure of nonpollinating wasps, or the seed dispersal syndrome is of great interest.

The monoecious hemi-epiphytic figs are particularly interesting for such studies. Not only are they diverse everywhere, but the existence of independent radiations in each major tropical biome invites investigation of macroevolutionary processes. Do hemi-epiphytes in Africa and the Neotropics show patterns of specialization to canopy strata similar to those found in Borneo? To what extent has coevolution with unrelated but ecologically convergent seed dispersers led to similar fruit designs? Has coevolution with different genera of pollinating and nonpollinating wasps followed similar evolutionary trajectories? Without a doubt, figs will continue to be fertile ground for testing and exploring ideas in evolutionary ecology for many years to come.

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